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BIOLOGICAL BULLETIN

ECOLOGICAL SUCCESSION.[1]

V. ASPECTS OF PHYSIOLOGICAL CLASSIFICATION.

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I. INTRODUCTION.

Every investigator appreciates the value of having several methods of organizing data on a given subject. Each new arrangement adds new light and often valuable conclusions.

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[1] The following errata appeared in the preceding paper, "Ecological Succession —IV.," Vol. XXIII., pp. 59 to 99 of this journal:

Page 66, Table I.: for *Lee* read *Dj.;* for *Psinida* read *Psinidia;* for *americanorum* read *americanus;* for *wyominganum* read *wyomingianum*; for *Cnemodophorus* read *Cnemidophorus.*

Page 67, for *arborens* read *arboreus* Say; for *Cyclisticus* read *Cylisticus;* for *Lyasopetalum* read *Lysiopetalum;* for *Spirobolis* read *Spirobolus;* for *promelia* read *pimelia;* for *Liobromum nigripalpi* read *Liobunum nigropalpi* Wood; for *hereculeanus* read *herculeanus;* for *Cerchus* read *Ceruchus.*

Page 68, for *melumboni* read *nelumbonis;* for *Ampulicidæ* read *Ceropalidæ;* for *Psithurus* read *Psithyrus;* for *anornis* read *anormis;* for *umbratis* read *umbratus;* opposite species 19 and 20, for *H* read *I.*

However in the general field of zoölogy, we have but one complete system of arranging data, namely the system of *taxonomy*. The recent attempts in ecology, while as yet scattered and incomplete, have been aimed in the general direction of the classification of organisms upon a *physiological basis with particular reference to relations to environment*. The relations of animals to environment were thought to be very orderly by many of the early naturalists but the lack of understanding of the environment led to difficulties. With the development of the idea of evolution, structural relations were sought, but aside from the "adaptations" of the large taxonomic groups to strata, etc., such attempts have, in the main, failed. The great importance which has been attached to the natural selection hypothesis has been largely responsible for the failure of naturalists to develop ecology along its proper physiological lines. This hypothesis, in the narrow sense in which it has been construed and applied, calls for life and death relations to environment, color and structural adaptations, and fixed physiological relations to environmental factors. Emphasis has been placed on the wrong phenomena; attention has been turned to pseudo-problems and some prejudice against all study of the environment and of the relations of the animal to the environment, has been developed.

On the plant side, present attempts at ecological classification date back at least to the publication of Warming's work in 1891, which followed closely after the general acceptance of the germ

Page 69, for *Byl* read *Gyl.*; for *fraudulentia* read *fraudulenta;* for *Pterostricus corecinus* read *Pterostichus coracinus;* for *Xylopodus saperaioides* read *Xylopinus saperdioides.* Table II., for *domocilorum* read *domicilorum;* for *Diaphoromera* read *Diapheromera.*

Page 70, for *Plectodera* read *Plectrodera;* for *Schistocera rubignosa* read *Schistocerca rubiginosa;* opposite species 11, for Locust read Pine.

Page 71, for *Tripleps* read *Triphleps;* for *guttivittata* read *guttivitta;* for *Scaphodius* read *Scaphoideus;* for *Lyngyphidæ* read *Linyphiidæ;* for *senitoria* read *senatoria;* for *Cryptophyllus perspecivius* read *Cyrtophyllus perspicillatus;* for *Symmirista* read *Symmerista;* for *anguissi* read *angusii.*

Page 72, for *obliturus* read *olitarius;* for *tubercolatus* read *tuberculatus.*

Page 82, for *Aglena* read *Agelena;* for *Dissostiera* read *Dissosteira;* for *Lyasopetalum* read *Lysiopetalum.*

Page 84, for *gracile* read *gracilis.*

Page 86, for *arborens* read *arboreus;* for *Tripleps* read *Triphleps.*

Page 97, for *'03*, Dahl, third reference, read *'08.*

Page 99, for *Woods-Jones*, read *Wood-Jones.*

plasm theory. This is, however, to be regarded as a renewal of interest turned aside at first by conflict with the church and later by the absorption of attention by the lines of work noted above, for the recognition of succession by Buffon preceded Darwin's "Origin of Speices" by one hundred and eighteen years (Cowles, '11) and occasional subsequent but early observations have strengthened the total evidence for this phenomenon. It is only a few years since we were regarding the environment as an ununderstandable hodge-podge. Now we must recognize that *environments are characterized by the most orderly of phenomena*, some of which were noted by early observers, and have often been verified and actually experimentally demonstrated during the last twenty years, by the plant ecologists. With this better understanding of the environments and the better knowledge of animal physiology, the relations of animals to environments considered physiologically appear particularly definite. Our knowledge is sufficient to enable one to indicate certain probabilities in this connection, which are based upon established principles.

In connection with the introduction of some of the principles of ecological classification and the logical necessities of such an attempt, the reader must not lose sight of the fact that there are, in practice, two points of view for investigation. One is that of evolution. The other that of physiology. One may make a physiological explanation of the behavior or structure of an organism and in no way explain its evolution, or on the other hand, he may contribute to the knowledge of the evolution of an organism without contributing to the knowledge of its physiology. This distinction is becoming less sharp with each year's progress in investigation, due merely to the adoption of physiological methods in the study of evolution and morphology. Again the reader must bear in mind the fact that regardless of widespread ideas to the contrary, *ecology* or *ethology* belongs primarily to the physiological point of view, and is therefore *outside of the range of criticism* from the point of view of *evolution* or the *current germ plasm doctrine.* Its frequent confusion with various branches of evolutionary speculation, such as mimicry, structural adaptation, etc., is one of the commonest errors of recent writers[1] and has been chiefly responsible for such prejudice as may possibly exist.

The definition of ecology, like that of any growing science is a thing to be modified as the science itself is modified, crystallized and limited. At present, *ecology is that branch of general physiology which deals with the organism as a whole, with its general life processes, as distinguished from the more special physiology of organs* (Semper, '81). With these limitations upon the term physiology, what may be termed *physiological life histories* (Ganong, '07) covers much of the field. Under this head fall matters of *rate* of *metabolism*, *latency* of eggs, *time* and *condition* of *reproduction*, necessary conditions for existence and especially *behavior in relation to the condition of existence.* Reactions of the animal maintain it in its normal environment; reactions are dependent upon rate of metabolism (Allee, '12, and citations) which may be modified by external conditions. Behavior reactions throughout the life-cycle are a good index of physiological life-history characters. If we knew the physiological life histories of a majority of animals most other ecological problems would be easy of solution. The chief difficulty in ecological work is our lack of knowledge of physiological life histories. On this account the relative importance of the different aspects of investigation given later in this paper is based upon present expediency.

Physiological life histories may, with elaborate facilities, be worked out in a laboratory. *Ecology* however considers physiological life histories *primarily in nature* and for this reason as has already been stated the central problem of ecology is the *mores*[2] problem or the problem of physiological life histories in relation to natural environments, the dominant facts in which

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[1] See *Trans. Am. Micro. Soc.*, Vol. XXX., p. 217.

[2] *Mores* (Latin, singular *mos*) "behavior," "habits," "customs"; admissible here because behavior is a good index of physiological conditions and constitutes the dominant phenomenon of a physiological life history in the sense proposed. We have used the term just as *form* and *forms* are used in biology; in one sense to apply to the general ecological *attributes* of motile organisms; in another sense to *animals* or *groups of animals* possessing particular ecological attributes. When applied in the latter sense to single animals or a single group of animals the plural is used in a singular construction. This seems preferable to using the singular form *mos* which has a *different* meaning and introduces a second word. The organism is viewed as a complex of activities and processes and is therefore a plural conception.

are facts of *behavior*, *habitat-preference*, *community* of habitat preferences and *laws governing* the *relations* of *organisms* in *communities*. The last is not a part of physiological life histories, the *mores* conception being broader than that of physiological life histories. An ecological classification is a classification upon a physiological basis, but since structure and physiology are inseparable, we must also note the relations of structure to ecology and to ecological classification.

II. Basis and Method of Classification.

1. *Basis.*

The ecological distribution of *mores* is the resultant of the behavior reactions of the animals constituting them, to variations of environmental conditions, encountered in their movements in space. According to the law of toleration (Shelford, '11[3]), the distribution of species or mores is limited by the variation of a factor or factors beyond the limit of toleration of the species or *mores* in question. The statement of the law was based upon field and experimental observations on the tiger beetles, which clearly supported this view. We noted that where the conditions were nearest optimum, the number of larvæ was greatest and where least favorable the number was smallest. It appears, from field study, that the number of individuals varies directly with the degree of deviation from the conditions most favorable. The distribution of each species or *mores* is probably representable by the ideal curve (see Fig. 9, *p.* 351) when viewed with reference to all environmental factors. As we pass in *different directions* from the point of maximum number of individuals, *different* factors or combinations of factors are seen to fluctuate. The area of maximum numbers is the area of overlapping of optima of the various factors. This is called the *ecological optimum* (Schimper, '03). The ecological optima of many mores are similar, a fact well known to naturalists. The fact is most evident where changes in conditions are most abrupt. Ecological classification places together groups of *mores* with similar ecological optima.

Ecological classification, whether of groups of individuals belonging to a single species, or of communities composed of all the animals of a locality without regard to their taxonomic relations, is based upon differences and similarities of *mores* or general physiological characters. These differences in *mores* are measured (*a*) by the direct study of the organism, and (*b*) by the study of the environment of the organism or the *mould into which the organism fits*. As a background for our point of view, we have, under the first heading, various experimental studies of adjustment of the behavior of organisms to surrounding conditions, especially studies of the modifiability of behavior, which has been definitely related to conditions which the organisms concerned encounter in their normal life in nature; under the second studies of the selection of habitat by organisms. My own studies (Shelford, '11[3]) from this point of view are at present very incomplete and serve to illustrate the methods only. Different tiger beetle species select different soils and as the females lay only one season, their first attempts at laying no doubt are the result of innate behavior (Shelford, '07). The work of many investigators (Wheeler, '10, *et al.*) confirms the general view that animals select their habitats upon the basis of characters more or less innate. The work of naturalists is important though it is defective mainly in that one often has difficulty in determining what habitat is meant.

A type of investigation which combines experimental and naturalistic consideration of the organism with analysis of the environment has been carried on by Allee ('12). He found that the rheotaxis of isopods of the same species occurring in both ponds and streams, is different in the two situations. He was able to change the pond *mores* to the stream *mores* by keeping pond isopods in stream conditions and vice versa. The agreement of the behavior of the animals of a habitat will be shown by a study of the behavior of the swift brook community now being conducted. There is a marked agreement of the animals of this community in their reactions to the factors encountered in the stream. This agreement is due (*a*) to the *selection of the habitat through innate behavior*, and (*b*) to the *adjustment of behavior to the conditions* through the effects of physical factors and through formation of habits and associations.

The study of the mould into which the organism fits becomes a *legitimate method as soon as the selection of habitat and the adjustment of behavior and physiological makeup, to the environment are shown to be general facts.* The study of the environment must be accompanied by studies of the *effects* of the *various factors* upon the *organisms* concerned. This is necessary if important factors are to be emphasized (Shelford, '12[1], p. 90; Shelford and Allee, '12).

2. *Ecological Specificity and Specificity of Behavior.*

We have stated that ecological classification is dependent upon *similarities* and *differences* in *mores* (physiological life histories, behavior, modes of life). We have noted also (Shelford, '12[1]) that there is *similarity* of mores within the same animal community and that the limits of animal communities are based upon similarities and differences of *mores.* Several questions at once arise. Is the same environment ever the same to different species? How much and what kind of similarity is to be expected? It is possible for two very different species to live under practically identical conditions, but probably this is rarely true in the same community, such cases usually being *separated geographically.* If the organs for the reception of stimuli, on the bodies of two animals living side by side, are differently placed, there must be obvious differences in reception of mechanical stimuli, light, etc. Indeed different species living under similar conditions may be sufficiently different physiologically to be differently affected by the same single stimulus, but ecologically, classification is based upon the *complete physiological life history,* mode of life, and behavior, so that differences in the effect of *single stimuli* cannot be too much emphasized.

It is quite clear to every naturalist, that within a given area, nearly every race or species possesses certain special peculiarities of structure and also of behavior, physiology, and mode of life. There is a large amount of specificity in the behavior of a species and as a rule, students of behavior have been unduly impressed by it. For example fishes (Shelford and Allee, '12) show a general community or similarity of reaction to such factors as carbon dioxide and other differences in water. The fishes turn back when they encounter increased carbon dioxide or other differences in dissolved content in the water, doing so without regard to the specific peculiarities of their behavior, such as methods of moving their tails, mouths or opercles. By way of further illustration, we note that, according to the accounts of naturalists, there are striking resemblances between the behavior of some of the antelopes of the savannas of Africa and certain of the savanna kangaroos of Australia. In other words certain kangaroos are ecologically similar to some antelopes. As has already been stated, the zoölogist is usually unduly impressed with specificities such as mode of movement of limbs, body, etc. Now if my reader pictures an *African antelope running gracefully from a pack of Cape hunting dogs* (Selous, pp. 119–123) *and an old-man-kangaroo leaping from a pack of dingoes* (Ward, '07, pp. 41, 243) *noting mainly the specific peculiarities of the movement of limbs and body of the pursued in each case*, he will be dwelling upon *specificities of little ecological significance and missing the point of view of the ecologist altogether.* These specificities of behavior are matters of little ecological significance; it matters not if one animal progresses by sommersaults so long as the two are in *agreement* in the matter of *reactions* to *physical factors* as indicated by the manner of *spending* the day,[1] *avoidance of forests, swamps, cold mountain tops, etc.*, entirely *available* to them, and in the mode of meeting enemies as indicated by the reaction to the approaching enemy—a relation to other animals of the community. As a further example, the specific method of avoiding stimuli shown by *Paramœcium* is not a matter of any considerable ecological importance. The chief argument against ecological classification is based upon specificity of behavior. With all the marked specificities there can be no similarities! Let us apply this logic to a few particular cases. Since there are specific differences in the behavior of different fish species, different fish species do not turn back from carbon dioxide in a similar way and are not similarly affected by it! Since there are species and no two species of a genus are alike there can be no genera; since there are genera each with definite characters, there can be no families, etc. *Specificity* of *behavior* comes in ecological classification or other ecological consideration as a matter of tertiary

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[1] Lydekker, III., 243; Vol. II., p. 322; Riverside, N. H., Vol. V., pp. 36–37.

or even quaternary significance, *even when details are being considered.* This applies to particular *mores* (ecological species) as well as to groupings of higher order. Ecological specificities are primarily *differences in physiological life histories manifested mainly by (a) details of time and place of reproduction and degree of latency in reproductive structures, and (b) by quantitative differences in reactions to the same intensity of the same environic factors.* Because of lack of knowledge of life histories, the latter will doubtless be most useful in practice. It is also the best test of animals temporarily invading a community to which they do not primarily belong. Such animals should be in partial agreement with the communities which they have entered even though their residence there be temporary.

3. *Stratification or Vertical Aspects.*

(*a*) *Adaptation.*—In the preceding paper we divided the animal communities into strata. Persons not familiar with ecology appear to think that structural adaptations are an important part of the consideration of modern ecology. In the first place, ecologists are skeptical of the significance of many if not of the majority of so called structural adaptations. In general, structural adaptations appear not to be correlated with the phenomena with which the modern ecologists are concerned. For example we note (Shelford, '07, '12[1]) four species of tiger beetles arranged in the horizontal series of conditions which we find at the south end of Lake Michigan. A careful study of the adults and the larvæ of these species fails to show any structural characters which are correlated with the conditions in which the species live. All have the same type of mandibles, the same kind of feet, and the same kind of ovipositor. There are no structural characters by which they can be located in their environments. The adults are structurally adapted to making holes in the ground with their ovipositors and thus depositing their eggs. The larvæ are adapted to a life in the ground. These are structural adaptations to *stratum.* All terrestrial tiger beetle species are somewhat in agreement as to adaptations. Other adaptations among the tiger beetles are adaptations for walking on leaves of plants (*Odontochila*, Bates, p. 169), for creeping on the trunks of trees

(*Derocrania*, Horn, '99, pp. 228–230), for depositing eggs in twigs (R. Shelford, '07). Apparently several of these types may occur, one above the other, in one locality, or at least at different levels in adjoining localities (R. Shelford, '02, pp. 233–234).

Among the Orthoptera we find forms adapted to burrow beneath the soil, others which live at the surface of the soil having ovipositors adapted to deposit eggs in soil, feet adapted to life on soil, etc. Those that live on the shrubs are adapted to walk on vegetation, and to deposit eggs in plant tissues (Morse, '04). Motile aquatic animals are adapted to burrow into the bottom, to cling onto the bottom, to cling on the vegetation or zoöphytes, or to swim about. Feeding adaptations in the fishes are to feed in the open water, in the vegetation, or on the bottom, each of which is a relation to stratum or matters comparable to strata.

Mammals are adapted to aquatic, subterranean, cursorial life. By way of further example, let us take the pocket gophers which occur (Merriam, 95) in the subterranean stratum of all the great steppes, deserts, and dry and moist forests of the United States and Mexico, apparently from the most arid deserts to the moistest tropical and subtropical forests. Adaptation limits their relations only to stratum. Again cursorial mammals, with all possible numbers of toes, are found in all of the climates of the world, in the forests, steppes, and deserts, arctic and tropic, all being adapted to the ground stratum. The arboreal types are likewise widely distributed. Arboreal monkeys, for example, occur from the snow covered pines of the Himalayas (Heilprin, '87) to the moist unchanging forests of the Amazon, all being adapted to the tree stratum. In many taxonomic groups, such as families and even genera, we find structural characters which seem fitted to various levels of habitats, but which do not limit the animal to any particular ecological *types* of plants growing in any particular set of physical conditions. Neither do they, in many cases, seriously limit its mode of activity. Adaptations to stratum appear in many cases to be quite elementary, occurring within genera, while other adaptations such as those for food getting, belong to larger taxonomic groups such as orders and suborders. Those of higher order are however never of primary ecological significance. Take the piercing mouth parts of the Hemiptera. This group occurs in every type of habitat from the marine pelagic to the ectoparasitic, and from tundra and desert to rain forest. All the chief principles of animal ecology could probably be illustrated by the Hemiptera, the sucking beak coming in only as a factor modifying the details, when we compare Hemiptera with Coleoptera which have biting mouth parts and similar habitat relations.

Such doubtful protective devices, as protective coloration, mimicry, aggressive coloration, etc., cannot be counted as any significant part of ecology until they are first established in fact and are shown to have some regular relation to reactions to environic factors or at least to activity. All of the chief typical cases that come under the head of protective coloration, mimicry, etc., are much shattered by such facts as are presented by Selous ('08, Ch. I. and II.).

(*b*) *Over-adaptation.*—If some animals are adapted, which implies that they are adjusted to a particular mode of life in their particular situation, in a way which is essential to a successful life in that situation, then other animals are over adapted (Coulter, '09, p. 62). Take an animal from the insect group, the dragon fly nymph, which has the labium modified as a prehensile organ and the maxillæ as additional mandibles. The posterior portion of the intestine is developed into a muscular cavity containing gills and serving as an hydraulic organ of locomotion. What is the advantage of all this specialization? The nymph appears to succeed no better than many other types with which it is in competition. It even appears clumsy and unadapted in many ways and is to the same degree *over-adapted.*

When we consider adaptations in relation to communities of organisms and to physical environments, with taxonomy thrown into the background, their significance loses force. Adaptation is adaptation primarily, when viewed from the standpoint of the structural type of the group to which the adapted organism belongs; it is an index of *taxonomic differentiation* rather than of *ecological relations.* The more important structural adaptations appear to be adaptations to *strata,* or matters of *specificity.* They have about the same significance among animals as the separation of plants into herbs, shrubs, and trees, has among plants. They merely represent, in the main, the different taxonomic groups primarily capable of occupying different strata or the like. Here and there an aberrant member has become adjusted in size or growth form to another stratum. Climatic grassland formations (Shelford, '11[3]) may perhaps be characterized by the absence of arboreally adapted animals but even here we may find exceptions, for *Didelphys azore* lives in grassland (Hudson, '03) but is unmistakably "adapted" to an arboreal life. Again in the rain forest of New Guinea, we find a tree kangaroo which is poorly adapted to arboreal life (Wallace, '69, p. 386).

When one brings together all the motile animals of a given stratum, in a forest or other type of habitat, and examines them with a view to classifying and generalizing concerning them, from the point of view of structure, he finds himself confronted with a hodge-podge of the so called "primitive," "adapted" and "unadapted," without the possibility of making any generalizations concerning them or of classifying them into structural ecological groups.

Among motile animals, structure must be considered in connection with activities, reactions, and general physiology as a limiting factor to be taken into account in many cases. It is often important in considering the ecological equivalence (Shelford, '11[3]) of similar communities or of the animals of the same community. Ecologically there is rarely reason for considering the structure of motile animals separate from activity. Accordingly it seems best to reject separate consideration of adaptation and to treat all questions of the structure of motile animals as *structures playing a rôle in the physiology and activity of the organism*. This includes all the important aspects without raising the question of adaptation or of the origin and genetic significance of such structures concerned. Even the relations of the animals to the strata are to be considered as *primarily physiological relations* to differences in *physical conditions*, such as were brought to attention in the preceding paper. Many animals invade two or more strata and are usually to be classed primarily in the stratum in which they breed. On account of this invasion of several strata, there is much overlapping of adjoining strata corresponding to overlapping of single characters in taxonomy.

4. *Habitat or Horizontal Aspects.*

Ecological classification is not only vertical but also horizontal. Some of the roughly horizontal aspects of classification, such as division into aquatic (marine and fresh water) and terrestrial (forest, prairie, etc.) are major aspects of classification long in use. Animals invade several of the minor recognizable *horizontal conditions less often than several of the vertical.* Still such overlappings are common, and as has already been noted, since overlapping of single characters is common in taxonomy, it cannot be urged as argument against ecological classification.

(*a*) *Large and Small Divisions.*—Considering terrestrial communities, the largest are those that occupy areas of relatively uniform climate (climatic, Schimper, '03: major; Adams, '08; Shelford, '11[3]). The smaller those of similar soil (including water) (edaphic, Schimper, '03), of similar degrees of exposure to wind, sun, etc. due to the topography (local or secondary, Adams, '08; Shelford, '11[3]). Each area when considered as an environment includes the vegetation, which is usually clearly different in growth-form in each area occupied by a different animal community.

Both local and climatic communities may be subdivided into still smaller but easily recognizable subdivisions. Their number is closely related to severity of climate, particularly with reference to moisture, and is greatest in the desert and smallest in the rain forest. For example, in dealing with forest development in the preceding paper (Shelford, '12[1]) we noted that in the earlier stages, conditions were dominated by the presence of *bare sand* open forest communities. The later stages were closed forest with the soil all covered and the character of the forest and of the animal communities quite *independent* of *soil* and *dependent* upon *climate.* Still each of these sets of conditions was divisible into several subdivisions, the sand dominated habitat into the cottonwood, the pine, and the black-oak habitats, each with a different rate of evaporation and each with different soil conditions along with recognizable differences in communities. The closed forest was likewise divisible into three habitats and three corresponding communities, the blackoak-whiteoak-redoak, the redoak-hickory, and the beech-maple.

(*b*) *Dynamic Relation of Local and Climatic Conditions.*—There are many local conditions in each climatic area. The relation of local conditions to the climatic or major is closely bound up with the principle of succession. In the preceding papers we have noted that succession may be due chiefly to physiographic changes, or to the fact that the organisms of a given stage affect conditions in such a way as to make their own continued existence impossible, and prepare the way for others. While in *particular cases*, *physiographic* conditions may dominate, in others *biological* conditions dominate. Both are probably always detectable factors. (Cowles, '11; Adams, '01, '08.)

Under the head of physiographic causes of succession come such processes as the uplifting and degradation of land, erosion, deposition, etc. Along a coast, the processes (Gilbert, '85; Gulliver, '99; Salisbury, '07) are causes of changes in physical conditions, material for abode, etc., and result in ecological succession. Such geological processes are treated in textbooks on geology and physiography and may be only outlined here.

When a body of land is uplifted or the level of the water into which it is drained is lowered, streams begin to work their way into the new land mass and cut deep valleys, with marked differences in both vegetation, physical conditions, and animal communities (Shelford, '11). The formation of numerous tributaries (see diagrams by Salisbury, Adams, '01) isolates portions of the upland in the form of hills. These hills are broken up into smaller hills by the smaller tributaries, and the resulting hills into still smaller, until the upland is all removed and the country reduced to a generally rolling topography with very little relief and known as a peneplain (Adams, '01; Salisbury, '08; Chamberlain and Salisbury, '06). The process of peneplanation then tends to fill all low lakes and ponds and to drain all high ones. It works over all of the materials of the upland and deposits them over much of the resulting surface, which tends to make the surface materials of a uniform nature. The processes involved go on in definite directions during longer or shorter periods and produce smaller and larger differences in conditions, due to topography, but all of these point toward a common end, the peneplain. Peneplains may be local being referable to some

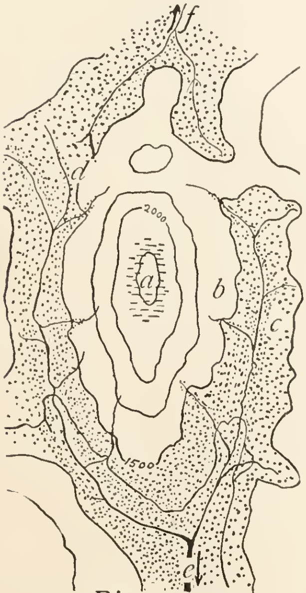

Fig. 1

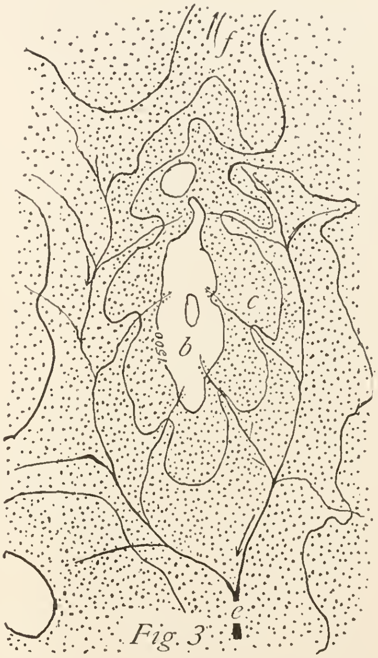

Fig. 3

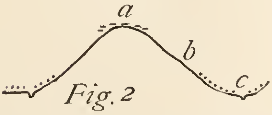

Fig. 2

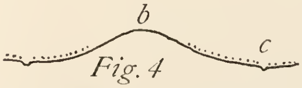

Fig. 4

FIGS. 1 and 2. Showing a mountain in east Tennessee [Briceville Folio, U. S. Geological Survey, Latitude 36° 30′ N. Longitude, 84° 5′ W. It is taken from the topographic map with some of the contour lines omitted. The contour interval is 250 ft. (80 meters)]. In Fig. 1 the area (*a*) indicated by the dashes is at the top of the mountain and represents the area covered by conifers. The blank area (*b*) represents the area of the mountain side covered with the oak and hickory forest the habitat of *Cicindela sexguttata*. The stippled area (*c*) represents the beech and maple in the valley. Fig. 2. Cross section of the same.

FIGS. 3 and 4. Showing the same mountain represented in Figs. 1 and 2, but in an hypothetical later stage, based on the supposition that the valley at the point (*e*) is at a peneplain level. In Fig. 3, stream (*e*) has cut through at the point (*d*) of Fig. 1 and captured the head-waters of the stream (*f*). The entire mountain has been sufficiently lowered to cause the conifer area to disappear entirely. The oak-hickory area is greatly reduced and the beech-maple is greatly increased, Fig. 4 is a cross section of the same (see Adams, '01).

large inland body of water like Lake Michigan (Atwood and Goldthwait, '08) or they may be extensive. In both cases the processes proceed in a definite direction.

In eastern North America, the topography of the Appalachian region is in the main features of importance in this connection, an erosion topography. In eastern Tennessee I found [as described by Cowles (unpublished)] that the tops of the mountains were frequently covered with conifers, the sides with oak and hickory, and the bases with beech and maple. In Figs. 1 and 2, the area marked with dashes is conifers, the blank area is oak and hickory, and the stippled area beech and maple. Each was occupied by different animal communities. The beech and maple are at a level at which the whole area will be when the mountain is reduced to a peneplain level (unpublished conclusion of Cowles). Hills with isolated patches of conifers at the top are numerous throughout the Appalachians. Hills covered with oak and hickory without the conifers, and surrounded by beech and maple and the other mesophytic trees that grow with these, were doubtless very common in the foothills of the Appalachians under primeval conditions.

Turning to Figs. 1 and 2 we note that as the height of the mountain is reduced the low beech area becomes larger, at the expense of the oak and hickory habitat, and the oak and hickory habitat in turn adds to itself at the expense of the conifers. In Figs. 3 and 4 is shown an hypothetical stage in which the stream has cut through the upland and captured the headwaters of the stream at point *d*. This has completely isolated the oak-hickory. It is completely surrounded by the beech and maple. The conifer community has disappeared. Peneplainations have taken place completely. For example, remains of ancient peneplains are recognized in the Appalachian region, each corresponding to a relative lowering of the level of the sea. The first was complete. The second was sufficient in extent to cause the isolation of numerous uplands and groups of mountains. The erosion processes now in progress have still further dissected the land into uplands of all possible heights, between the upper and lower limits. Each peneplanation was accompanied by changes in physical conditions, in vegetation and by ecological succession of animal communities (Adams, 01).

Succession proceeds until conditions are such as to be favorable to organisms which are immune to their own effects upon their own environment. Ecological succession proceeds from all *mores* types toward the physiological types of organisms which are adjusted to climatic conditions of the area. On the basis of good evidence, which cannot be reviewed here, but which is to be found in the writings of Cowles ('01[1], '01[2]; Clements, '05; Gleason, '08, '11; Adams, '08[1], '08[2]; Whitford, '06) and others, botanists have reached the conclusion that the vegetation and therefore the chief animal habitats of the local conditions are

SAND RIDGE
V, A, 1—Cottonwood
V, A, 2—Gray pine
V, A, 3— { Black oak
V, B, 1 { White oak
V, B, 2 { Red oak
Hickory

CLAY BLUFF
Aspen } near
Cottonwood } IV, B.
Hop-Hornbeam }
White oak } V, B, 1
Red oak }
Hickory } V, B, 2

[*Rana sylvatica Association*]
BEECH AND SUGAR MAPLE, V, B, 3
[*Rana sylvatica* Association]
Tulip Hickory } V, B, 2
Basswood Red oak }
White elm and white ash Bur oak
IV, A, 2 { Swamp whiteoak Bass-wood
Buttonbush Hawthorn
II, C, 2 { Cat-tail and Bulrush Slippery elm and white elm
Water lily and Water Mill-foil River maple
II, C, 1—Chara Black willow—IV, A, 1
POND FLOOD PLAIN

FIG. 5. Showing convergence of four types of habitats in northern Indiana to the beech and maple forest. Prepared with the assistance and from the writings of Dr. H. C. Cowles. Read from the extremes toward the center. The figures and letters standing outside the names of the trees refer to the communities similarly numbered in the list on pp. 358 and indicates the plants with which they are associated. The absence of numbers in connection with a number of the plants is due to the incompleteness of the lists in question.

converging toward a climatic type immune to its *own excretory products*. This has been called the climatic climax. The diagram (Fig. 5) shows some of the striking stages in convergence in northern Indiana. See also diagrams by Gleason ('08, p. 78, and '10, p. 133).

The principle of convergence, while not generally established is believed to be of wide application. It has been suggested, in connection with the tropical forest about Mount Marivales, in the Lamoa Forest Reserve (province of Bataan, island of Luzon, P. I.; Whitford, '06) where the rainfall is great. Here the difference between the vegetation of a ravine and the adjoining upland is less than in the temperate regions. The principles are, however, the same as those established in the temperate regions of America, Fig. 6.

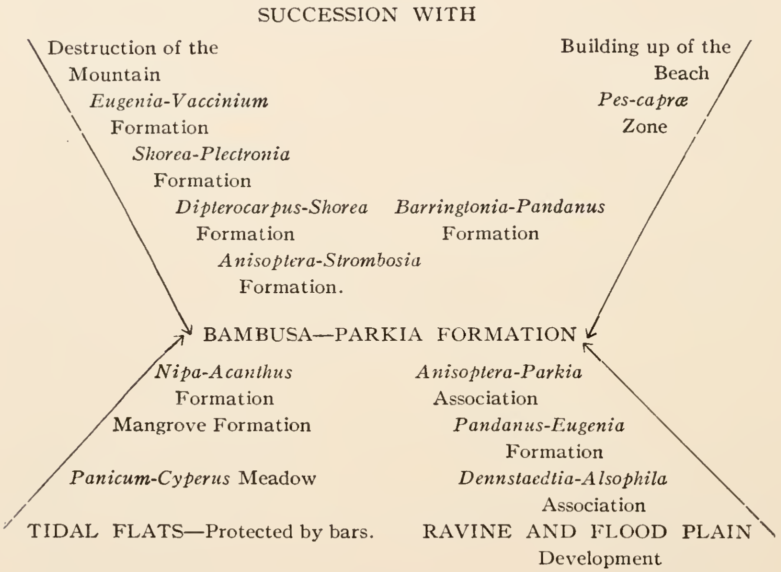

FIG. 6. Showing succession and convergence in a tropical climate. Read from the extremities toward the center. Beneath the word "mountain" is shown the succession of formations with peneplanation; beneath "beach" with the building up of the beach (when it has been built up above high tide, the succession proceeds without physiographic change); above "ravine" and "flood-plain," and above "tidal flats," succession with the development and final destruction of these features. Compiled from Whitford's account, with the assistance of Dr. H. C. Cowles.

Whitford's statement regarding the climax forest of this tropical area is as follows (p. 679): "The physiography of the entire mountain is very unstable and therefore the vegetation is temporary. With its (the mountain's) destruction, it will pass to a more and more permanent condition and the vegetative types will be altered with the change in the topography; the climate will then also be different, and will more nearly approximate that at present prevalent at the base; therefore the erosive topography at old age will have a vegetative condition not unlike the *Bambusa-Parkia* formation. Just before the death of such a topography, the whole country will be brought nearly to base level (peneplain) with the ground water near the surface. The vegetative conditions will not be unlike that of a delta region, of which there are many fine examples in the Philippines. . . . Of course the above are only theoretical considerations, yet these erosive stages are approximated in different parts of the island, so that when logically united, the genetic relations of the different vegetative formations can be made clear."

Physiographic processes and the processes of plant succession go on at varying rates under different conditions. Where the land stands low, is of easily eroded material and in a rainy district, a peneplain may develop over a considerable area in a few thousand or even hundreds of years. The same process would require infinitely more time in an arid region. With favorable soil conditions, a shallow pond will pass through all the stages of succession and into prairie or early forest in two or three decades. In moist climates, young forest springs up in a comparable period. On the other hand, the peneplanation of large areas, climatic changes, etc., require longer periods but *follow* the *same general laws as do those changes which take place quickly*, and ecological succession is similar in principle no matter whether the changes are slow or rapid. *Animal habitats and animal communities are orthogenetic and converging* (Adams, '08).

5. *Primary and Secondary Conditions and Communities.*

Every system of agriculture is, ecologically speaking, the holding back of all natural changes due to the effect of organisms. It consists in preventing the operations of all the biological laws, by which changes in the character of the habitat are brought about. If the organization of ecological materials is to be brought about in correlation with natural laws, then *agricultural* communities are essentially *useless* subjects for study.

Plant ecologists have recognized a division into primary and secondary communities (Warming, '09). The *primary com-*

munities are those which are normal to a given geographical area, while the *secondary communities* are those produced by cultivation or other activities of man, and are maintained only by cultivation, reverting to the primary types as soon as the cultivation ceases. They therefore represent ecological experiments with the essential records usually entirely lacking, and with the habits of the species constituting them undetermined, so that until the primary communities have been thoroughly investigated, the value of such experiments cannot be ascertained. Failure to recognize the division into primary and secondary is responsible for much of the confusion in the matter of environmental relations of animals in general, but more especially of land animals.

hed tih thyr eghreth bgrti
rty dbhty fbhtygfh dbgfty
dftr fgythrtg bfgtyr hufgk
fgvcyhtuyfgtry vbgft rytgm
cvdfrterfdyhtub vnhgythubb
bcvfdtxnzxdfcrtfbhtgydbfgg
vb fnhtbgfy fgyr bfgvdftrt
bfgtrybdbfghty vbft dgtrxd
vbgf tg fbgtyhyuijghb f nb
dfcrgtryhfy vbgfhty dbgfty
cbvfghtygdtfrnvkjgh fbgtb
cvfdgfbt nhkzxdscxgczkzkvg
bfgtyhr dftrgtybvhfgiingvb
dfcrg cgbfhty du bkbkbbgfh

FIG. 7.
Showing the arrangement of plants and animals on a plot of ground under primeval conditions, each letter representing several closely associated plants and animals.

edge rftfgyrhtubfhgtybgft
fecdftrybthuginf dvgfhytb
cb a a a a a a a a a a bf
ed a a a a a a a a a a ed
fg a a a a a a a a a a fg
dc a a a a a a a a a a dc
eb a a a a a a a a a a dg
fd a a a a a a a a a a fd
dc a a a a a a a a a a dc
fe a a a a a a a a a a fe
eg a a a a a a a a a a eg
fc a a a a a a a a a a fc
cgnvdftrgghhfgdbfbdgtrycg
gfzcvdg cvbdg fvgty ggd b

FIG. 8.
Showing the arrangement under agricultural conditions. Some of the original groups are to be found along the fence rows.

When civilized man first enters a new territory, he destroys or attempts to destroy, large game which threatens him and his domestic animals. He then destroys the natural vegetation and incidentally many other animals, by clearing the timber and burning all woody débris, and plowing and putting out plants which are entirely new to the region. Under primeval conditions plants are arranged irregularly as roughly indicated by the letters in Fig. 7. After the land is put to agricultural uses, they are arranged as in Fig. 8. Here the plants are all of one kind and are arranged in rows. A grove of the original vegetation is sometimes left, and some of the original plants remain near the fences, etc.

The fence rows and road sides are usually inhabited in the forested districts, and often also in the prairie by forest margin animals. The weedy, shrubby roadside and fence row is duplicated in the abandoned fields which are common on the poorer soils. In a forested area, some forest animals live after the clearing process is finished, in fence corners, under stones, etc. The distribution of a given species with respect to *conditions* is representable as the solid of an ideal curve, Fig. 9, the modal portion of the curve being the optimum conditions for the species in the forest. When the forest is removed, if we assume that the species can still live for a time, we find it in several different situations, which represent the outskirts of the range of toleration. Such places are protected ravines with bushes, fence corners, and partially cleared woodland. None of the situations lies within

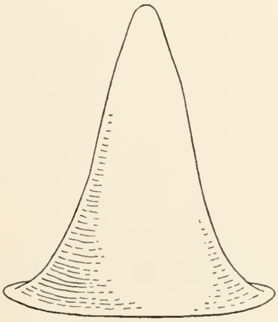

Fig. 9

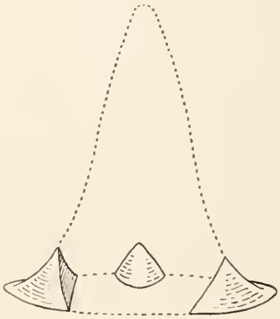

Fig. 10

Fig. 9. The solid of an ideal curve, representing the distribution of numbers of individuals of a *mores* with respect to degrees of variation of environic factors in space but without reference to distance or area covered by the degrees of variation. The central or modal portion is the area of ecological optimum.

Fig. 10. Showing the distribution of the same *mores*, after the natural vegetation has been supplanted by agricultural plants and the *mores* has been left in the fence rows, roadsides, ravines,—situation which represented the outskirts of its possible range under primeval conditions.

the area of optimum. A study of the ecological distribution of the animals thus located gives no correct idea of the ecological optimum, but makes the relations of the species to conditions seem *particularly variable.* From the point of view of ecological generalization, data on distribution under agricultural conditions are of questionable value.

6. *Development of Ecological Classification.*

The separation of animals into marine, fresh-water, and terrestrial has long been practiced; such a classification has about the same significance as the division of animals into vertebrates and invertebrates. Some other divisions have been recognized but usually rather loosely and little could probably be added by the study of literature which exists. A few of the recent attempts at ecological classification deserve mention. Three principal classifications by zoölogists apparently not in close touch with progress on the plant side must be noted. Morse ('08) divided the Orthoptera into *geophiles* and *phytophyles* representing certain "structural adaptations" (to strata). Both of these main groups he further divided into *xerophiles* and *hygrophiles*, and each of these in turn into *campestrian* and *sylvan*, etc. The classification is dependent primarily upon strata. The factors involved are unanalyzed and the scheme fails to distinguish the differences in physical conditions, which will probably come to be the basis for all ecological classification. For example, shrub-inhabiting species are not divided into those inhabiting *thickets exposed to sun and atmosphere in the open* and those inhabiting thickets or shrubbery in the *shaded forest.* Two groups wholly unlike in their relations to physical factors are thus put together. Shull ('11) points out the failure of the classification in practice.

Hancock ('11) follows a plan similar to that of Morse but makes it much more complete, on the whole, contributing much to the knowledge of ecological distribution of the Orthoptera. He fails, however, to separate primary (primeval) conditions from secondary (agricultural and human) conditions, and like Morse, has made divisions primarily upon the basis of strata or levels, with only partial consideration of physical factors or physical conditions. A reviewer (Pearse, '12) of Hancock's book (Shelford, '12) appears to have thought that this classification followed that of plant ecologists, but the main difficulty with this classification and that of Morse, is that they do not follow the plant ecologists' classification in any of its essential features. Both made the primary division vertical, though frequent invasion of several strata by the same animals makes the application of such a system to entire communities a practical impossibility. Such invasions of the recognizable horizontal divisions are far less frequent. Dahl ('08), in a list of places from which animals may be collected, gives a good classification of animal habitats and partially separates the primary and the secondary conditions. His general outline possesses many points of merit, and is probably the best published list. The author's comprehensive knowledge of the subject is clearly indicated throughout. It is not, however, arranged with particular reference to physical factors, and differs from the attempts of the American ecologists in that it is not based upon the laws of evolution or succession of environments.

The advantages of following natural laws, in ecological classification, should not need elaboration, for such has been the chief guide of all systems of classification of scientific data, at least since the time of Darwin. Elements of progress in ecological classification, following natural laws governing animal and plant habitats, have come chiefly from American ecologists, and largely, no doubt, because in the newer country there has been more opportunity to study the laws of succession. In Europe such laws can more rarely be studied, because of the more intensive efforts of man to prevent the operation of such laws.

In this country, Cowles was the first to make use of the laws governing plant habitats, in the classification of plant communities. Warming who contributed to the field before Cowles, took the condition of the plant as his main guide, but clearly recognized the laws governing habitats as of importance. Clements has also added much on the plant side.

Adams ('08) and Gleason ('08) arranged the animal communities of Isle Royale, Lake Superior, according to laws of succession, and gave us important elements of progress. Livingstone, Brown, Transeau, and Shimek have made comparative studies of the rate of evaporation in different habitats. Fuller most recently has studied the rates of evaporation in well understood stages of forest development which we discussed in the preceding paper. The sum total of evidence at hand indicates that the laws of succession and the physical conditions on the one hand and *growth-form* and *mores* on the other *are very generally in accord.*

Ecological classification of animals must be based upon community of physiological makeup, behavior, and mode of life. Those natural groups of animals which possess likenesses are the communities which we must recognize. One community ends and another begins where we find a general more or less striking difference in the larger *mores* characters of the organisms concerned.

7. *Ecological Terminology.*

Terminology in ecology is still unsettled and changing. Groupings have thus far been based upon similarity of habitat. Habitat likenesses have, in general, been based upon general resemblances. General resemblances have not always been accompanied by similar physical conditions, as was pointed out in the preceding paper of this series. In general, there has been an agreement in the recognition of strata, of associations as communities based upon the minor differences in habitat, and formations based upon the larger major differences in habitats. Dahl ('08) uses the term zoötope for formation and biocönose for association and apparently stratum also. Clements uses consocies for a division of a community dominated by some one species of plant; the term in this sense is less applicable to animals than to plants.

We give the communities of different orders below with taxonomic divisions of corresponding magnitude opposite, for comparison. With the exception of the first, these taxonomic groupings do not bear the slightest relation to the ecological groupings, but are added to indicate magnitude.

Mores (the term applied to animals possessing certain attributes) are groups of organisms in full agreement as to physio-

Dahl ('08)	Plant and Animal Ecologists	Taxonomic Groups.
Form	(Mos) mores (Shelford, '11)	Form (forms) (Species).
	Consocium (Clements, '06)	Genus.
Biocönose	Stratum or Story (Warning)	Family.
	Association or Society (Warning)	Order.
Zootope	Formation (Grisebach, '48; fide Clements).	Class.
	Extensive or Climatic Formations	Phylum.
	(Aquatic and Terrestrial.)	Vertebrates and Invertebrates.

logical life histories shown by the details of habitat preference, time of reproduction, reactions to physical factors of the environment, etc. The organisms constituting a *mores* usually belong to a single species but may include *more* than one species as *specificities of behavior* are not primarily significant (see p. 338).

Consocies are groups of *mores* usually dominated by one or two of the *mores* concerned and in agreement as to the main features of habitat preference, reaction to physical factors, time of reproduction, etc. Example: the prairie aphid consocium; the aphids control a group of organisms which for the most part prey upon them, as for instance, certain species of lace-wings, lady beetles, syrphus flies, etc.

Strata are groups of *consocies* occupying the recognizable vertical divisions of a uniform area. Strata are in agreement as to materials for abode and general physical conditions, but in less detail than the consocies which constitute them. (For differences of physical conditions see Table V., p. 84; Shelford, '12). For example, the beech forest animal community is clearly divisible into the subterranean-ground stratum, field stratum (level of the tops of the herbaceous vegetation), the shrub stratum (level of the tops of the dominant shrubs), the lower tree stratum (level of the shaded branches of the trees), and the upper tree stratum. A given animal is classified primarily, with the stratum in which it breeds, as being most important to it, and secondarily with the stratum in which it feeds, etc., as in many cases most important to other animals. The migration of animals from one stratum to another makes the division lines difficult to draw in some cases. Still the recognition of strata is essential though a rigid classification is undesirable. Consocies boring into wood of living trees, probably, should be considered as consocies relatively independent of stratification phenomena.

Associations are groups of strata uniform over a considerable area. The majority of *mores*, *consocies*, and *strata*, are different in different associations. A minority of strata may be similar though rarely identical. The unity of associations is dependent upon the migration of the same individual and the same *mores* from one stratum to another at different times of day or at different periods of their life histories. Such migration is far less frequent than from one association to another.

Formations are groups of associations. Formations differ from one another in all the strata, no two being closely similar. The number of species common to two formations is usually small (*e. g.*, 5 per cent.). Migrations of individuals from one formation to another are relatively rare.

To illustrate associations and formations, we have noted two great groups in the forest development series discussed. These groups are the cottonwood, pine, blackoak associations belonging to the sand area and in disagreement in the majority of *mores*, consocies, and strata; and the redoak, hickory, and beech associations belonging to the climatic forest proper and comparable with the first group in disagreement. The *mores* of the former are characteristic of sand areas, within the range of the deciduous forest climate. On this basis we may designate this as the *sand area animal formation of the deciduous forest climate* (Gleason, '10). It is here made up of the three *associations* just mentioned. The three later stages constitute the *deciduous forest animal formation*, which is here also made up of the three animal *associations*, named above. The two formations are separated upon the basis of striking differences in modes of life of the animals of the sand-dominated and forest-dominated communities and are in general disagreement as to *mores*, consocies, and strata concerned, only about 5 per cent. of the animals of the two hundred species listed in the preceding paper occurring sparingly or occasionally in the more similar associations of the two formations. The character of these differences was briefly outlined on pages 89–90 of the same paper (Shelford, '12[1]).

Extensive or climatic formations are groups of formations including all clearly influenced by a given climate in the case of land formations and (if recognizable in fresh water) by *topographic age* of a large area and by climate in the case of aquatic formations. For example, all of the thicket and other early stages of forest development of the area dominated by the deciduous forest formation constitute the deciduous forest extensive formation. Such formations occupy large areas which may be termed *ecological provinces* (Gleason, '10).

8. *Animal Communities in the Forest Border Region.*

The forest border region is the western line of demarkation of the deciduous forest climate. The following is a list of some animal communities about the south end of Lake Michigan. It is not intended to be complete, but rather to illustrate the use of the terms with particular reference to the communities mentioned in this series of papers.

- I. Stream Communities.
  - A. Intermittent Stream Communities.
    - 1. Horned Dace or Pool Association.
  - B. Permanent Stream Communities.
    - 1. *Hydropsyche* or Riffle Formation.
    - 2. *Anodontoides ferussacianus*—Sand or Gravel Bottom Formations.
    - 3. Baselevel or Sluggish Stream Communities.
      - *a.* Pelagic Formation.
      - *b.* *Hexagenia lineata* or Silt Bottom Formation.
      - *c.* *Planorbis bicarinatus* or Vegetation Formation.
- II. Lake-Pond Communities.
  - A. Pelagic Formations.
  - B. *Pleurocera subulare* or Terrigenous Bottom Formation.
  - C. Vegetation Formation.
    - 1. *Leptocerinæ* or Submerged Vegetation Association.
    - 2. *Neuronia* or Emerging Vegetation Association.
  - D. Temporary Pond Formation.
- III. Prairie or Grassland Formation of the Savanna Climate.
  - A. Grassland Associations of Moist and Marshy Soil in the Savanna and Forest Climates.
  - B. Prairie Chicken or Prairie Associations of the Savanna Climate.

- IV. Thicket or Forest Margin Formations of the Savanna and Forest Climate.
  - A. Wet Ground Thicket Associations. (Lower strata occasionally submerged.)
    - 1. River Deposit (Silt) or Stream Margin Thicket Sub-formations.[1] (First stage in the development of Flood Plain Forest.)
    - 2. Marsh and Pond Margin Thicket Sub-formation. (First association in the development of forest in marshes.)
    - 3. Candle-head or Moist Forest Margin or Thicket Sub-formation of the Savanna and Deciduous Forest Climates.
  - B. *Straussia longipennis* of High Forest Margin Associations of the Savanna Climate. (A climatic association of considerable permanency.)
- V. Forest Communities of the Deciduous Forest Climate.
  - A. Formations on Sand in the Deciduous Forest Climate or Province.
    - 1. *Cicindela lepida* or Cottonwood Association.
    - 2. *Cicindela Lecontei* or the Pine Association.
    - 3. Ant Lion or Black Oak Association.
  - B. Climatic Forest Formation of the Deciduous Forest Climate.
    - 1. Blackoak-Redoak Association.
    - 2. *Cicindela sexguttata* or Redoak-Hickory Association. (1 and 2 were treated together in the preceding paper and in the discussion above but may readily be separated.)
    - 3. *Rana sylvatica* or Beech-Maple Association.

Each division made here is based upon observations on the ecology of the animals constituting it. Marked differences in

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[1] The term *association* is applied mainly to stages in the development of climatic and of old topography formations; *subformation* (Warning), to communities comparably different physiologically but not clearly genetically related, or to associations when no genetic relationships are implied. Thus here in a classification intended to be primarily physiological, the stream margin thicket is placed among the thicket formations while in a purely genetic classification as shown in the chief features of arrangement in Fig. 11 it would be termed a stage or association in flood plain forest development.

mode of life, reaction to physical factors, time of seasonal appearance, are noticeable between the formations and lesser differences of the same sort between the associations.

We note from Fig. 11 showing the relation of communities, that intermittent streams become permanent, gravel bottom gains ascendency over riffles and silt bottom over gravel bottom, which is accompanied by a decrease in strength of current. All types of streams converge to the base level stream, all large lakes toward small lakes, which are parallel with the sluggish streams. These small lakes become ponds and finally dry land, in the forest border region, either prairie or forest. Forest margin or thicket is a tension line and may shift position rapidly.

The relation of the different habitats is a genetic one, the most permanent habitats being the sluggish stream and climax plant communities. Each is characterized by *different mores*, and as the one habitat is transformed into another the *mores change accordingly*.

III. General Discussion.

The environmental processes, which we are discussing are those in which organisms have existed since their origin on earth. The stresses and strains to which organisms have been subjected have been in the same direction for long periods. Now that we have learned much concerning organic response to environment, such as physiological response, behavior response, and structural response, we note at once that processes of adjustment and equilibration of living substance may bear important relations, on the one hand to environmental processes and on the other to the physiological aspect of biological phenomena. Ecological classification is then worthy of attention.

With all of their imperfections and uncertainties, the ideas of phylogeny which are presented in our phylogenetic system of taxonomy are an important asset in zoölogical thinking from the point of view of structure and development. The classification which ecologists are striving to build up will serve a purpose in behavior, physiology, and ecology, analogous in this respect to that served by the phylogenetic classification in morphological thought. It should however be flexible rather than rigid and

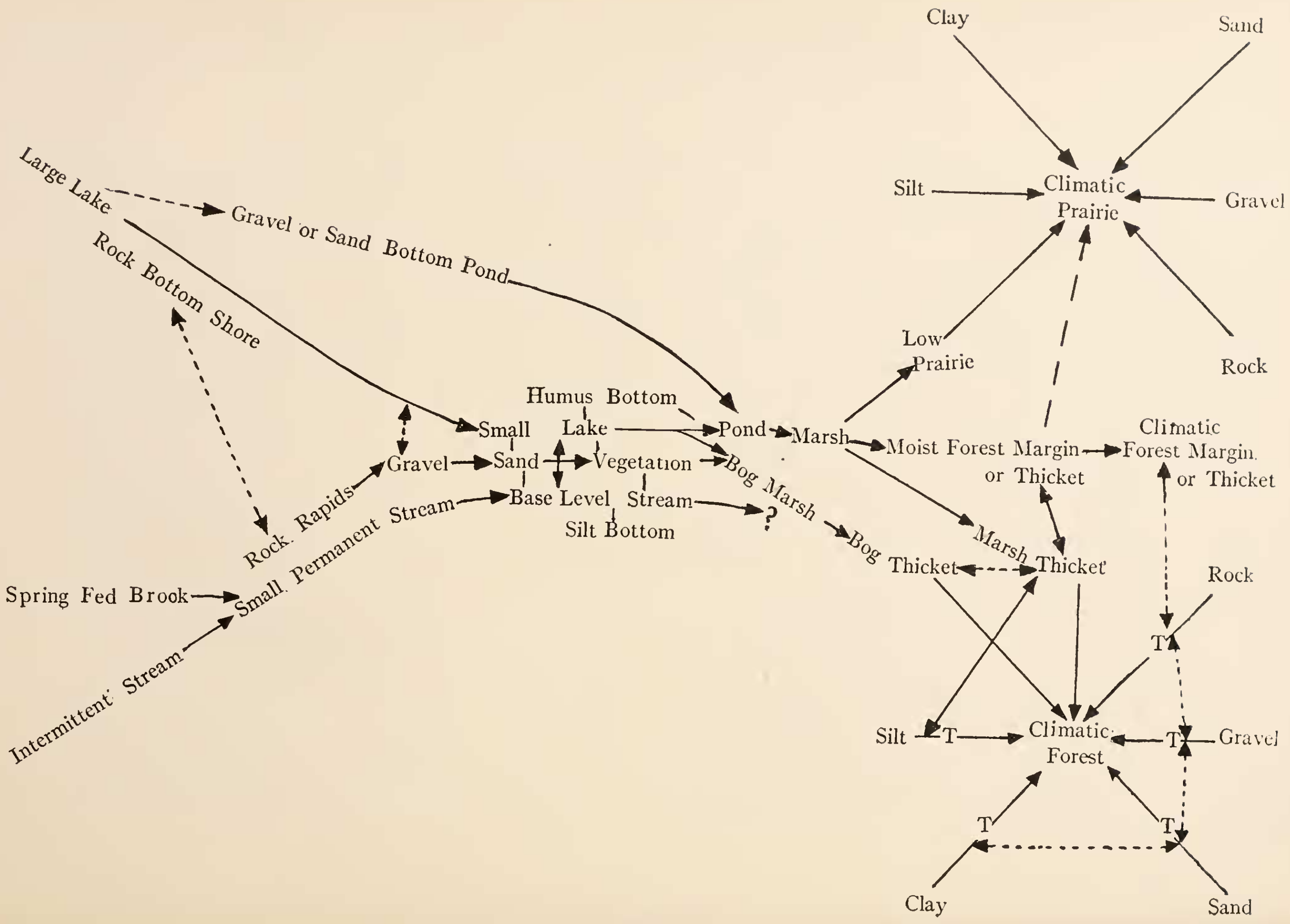
Large Lake
Gravel or Sand Bottom Pond
Rock Bottom Shore
Spring Fed Brook
Intermittent Stream
Small Permanent Stream
Rock Rapids
Gravel
Small
Sand
Base Level
Humus Bottom
Lake
Vegetation
Stream
Silt Bottom
Pond
Marsh
Bog Marsh
?
Bog
Thicket
Low Prairie
Moist Forest Margin or Thicket
Marsh
Thicket
Climatic Forest Margin or Thicket
Clay
Sand
Silt
Climatic Prairie
Gravel
Rock
Rock
T
Silt
T
Climatic Forest
T
Gravel
T
T
Clay
Sand

FIG. 11.

FIG. 11. Showing some relations of the chief animal communities of the forest border region of central North America. The word community or communities is to be understood as following all of the words or phrases appearing in the diagram. Single pointed arrows show the directions of succession, double pointed arrows show similarities of conditions and the occurrence of several or many of the same species in considerable numbers in some of the strata of communities between which such arrows extend. Broken lines indicate less definite relations than the solid lines. Starting with the aquatic communities we note that spring fed and intermittent stream communities converge with physiographic ageing to small permanent swift stream communities and permanent swift stream communities are succeeded by base level stream communities. The characteristic communities of small permanent streams and base level streams are indicated above them. Taking up another line we note that the large lake communities are succeeded by the small lake communities. Rocky shore communities of the large lake have features in common with those of the rocky rapids of the stream. The sand, gravel and vegetation communities of the baselevel stream and the small lake have many things in common, while the silt and humus bottom communities are distinguishing features of the two. Communities of ponds originating by very rapid physiographic changes pass through a series of stages comparable to those found in the different parts of the small lake. The lake communities pass to the pond community stage or give rise to a floating bog marsh community which is displaced by a floating bog thicket community. Cowles states that this takes place in deep lakes while the shallow ones become ponds which give rise to marshes with firm substratum; the marsh community may be displaced wholly by a low prairie community, in part by a thicket or forest margin community or wholly by a thicket community which will be succeeded by a forest community. In the savanna or prairie climate the marsh margin thicket may become a climatic thicket or forest margin. In the savanna or prairie climate the communities of all the various soils and the low prairie community may converge to the climate prairie community, or to the forest community as is shown below for the forest climate. In the forest climate and locally in the savanna climate the communities of all the various soils pass through a thicket community stage (*T*) related to a climatic forest margin. The thicket communities of all the dry soils are related to the forest margin or thicket community of the savanna climate.

true to fact rather than to schemes. Figuratively speaking, an ecological classification cuts taxonomy vertically, showing many structural adaptations as matters of stratum. It also cuts it again horizontally, showing ecological similarity in organisms, structurally and phylogenetically diverse. It therefore provides a new and different means of organization of data.

What is the significance in the fact (Shelford, '12^1) that *Cicindela lepida* belongs to the ecological group, the cottonwood association, which we may say corresponds to an order, and to the subterranean ground stratum (corresponding to family) and to the *Cicindela lepida mores?* Furthermore that *Cicindela lecontei* and *Cicindela sexguttata* belong to respective different and older situations or associations? We note that the habitats in which the species occur are characterized by distinctly different soils, moisture, amounts of shade and light. We note furthermore that these animals are possessed of unusual powers of flight and are able to *select* conditions suited to their physiological constitution. Their *mores* characters are definite characters, which can be measured in terms of reactions to measured complexes of physical and other environmental factors. They are as clearly defined as any morphological taxonomic characters and can be measured with the accuracy of physical phenomena.

Doubtless to the student of genetics, the question of the origin of such characters and their fixation in heredity is a leading question. At this point we know little or nothing. Since nearly all species have definite habitat preferences and since many varieties differ slightly from the related species form in the matter of habitat preference, it is probable that origin of a slight change in habitat preference, meaning a slight change in *reaction* to *physical factors*, a *change in ecological optimum*, is usually an early correlative of the origin of new races. Still the so-called taxonomic characters may remain apparently unchanged while marked changes in habitat preference and in reaction to physical factors are being brought about in plastic animals (Allee, '12, p. 341). On the other hand, the segregation in the so-called pure lines and races, accomplished in experimental breeding, often appears to take place without any regard to environment (Cockerell, '08, p. 547). These two facts accepted as they stand are in full accord and we might conclude that there are no relations between primary ecological characters and taxonomic characters. Such however can hardly be strictly true, but we cannot see what the real relations may be. If our point of view of ecology is correct the *ecological* characters of a race experimentally segregated, or experimentally produced must in practice consist *primarily* of *reaction to physical factors* or *combinations of physical factors* or to entire environmental complexes, secondly of a definite rate of metabolism, time of appearance or the like, thirdly of specificity of behavior, and fourthly of structural characters modifying behavior (see p. 339, order that of expediency). Relatively fixed taxonomic integumentary characters have no bearing on ecological matters, not even according to the broadest definitions of the subject. The characters which are not related to the environment, and which are of no ecological value, are the ones quite generally used in breeding work, specificity of behavior standing second, and plastic structure third, *primary ecological matters usually receiving no adequate attention or only such attention as comes incidentally with the handling of the material;* the results consisting of noted differences in reaction to light of doubtful intensity and quality, or similar temperature differences, etc. The testing of primary ecological characters can be adequately conducted in three ways. First, by the measurement of reaction to all or several of the chief environmental factors under rigidly controlled conditions, with each factor accurately measured qualitatively and quantitatively, and with the measurements of the speed or intensity of the reaction repeatedly determined. Second, by testing the reaction of the animals to a graded environmental complex of known constitution, and third, by putting the animals out into a graded series of natural environments selected with due reference to the species in question. Being easily open to experiment, the question of the relation of taxonomic and ecological characters should be left for experimental studies to answer.

The relation of habitat preference to the so-called structural adaptations and to their origin is, as we have seen, not intimate, and the method of experimental attack less obvious than in the case above. In 1907 we attempted to point out possible relations of succession and isolation, to adaptations to strata.[1]

Turning to the tiger beetles to illustrate a mode of analysis of adaptation characters, we note that the entire family of Cicindelidæ is characterized by the same general type of mouth parts, same type of larvæ (R. Shelford, '07; V. E. Shelford, '08). Ovipositors, feet, and larval structures are somewhat different in the arboreal and terrestrial forms. The arboreal mode of life occurs at least so far as the adults are concerned, to a greater or less extent in each of the great tribes (Horn, '08, '10). The genera *Collyris* (Horn, '08, p. 99), *Pogonostoma* (*l. c.*, p. 86), and *Ctenostoma* (*l. c.*, p. 89) are quite generally arboreal (Horn, '08, '10). While the mode of origin of existing arboreal habits must remain a matter of conjecture from which we cannot hope to eliminate elements of subjective fancy, and while it is probable that representatives of arboreal groups have become terrestrial and vice versa, still the ground inhabitants are by far the most numerous and most like other Coleoptera. The differences between ground forms and ectophytic forms are clearly *more elementary* than such characters as mouth parts, general larval or ovipositor characters, because the former consist of *minor modifications* of these general characters. If the problem of adaptation may be attacked directly at all, we must first separate the *smaller* from the *larger adaptation* characters. This accomplished we must note the kinds of conditions to which the adaptation characters are related. In the case of the tiger beetles, as will be found to be true in many other cases, the more *elementary characters are adaptations to stratum.*

As succession proceeds, as we have noted in the preceding paper ('12[1]), conditions become progressively less favorable on the ground, for many animals, and the terrestrial members of the various groups give way to ectophytic forms of higher and higher levels. We have already noted that the process of peneplanation in the deciduous forest climate causes isolation of uplands with oak hickory forest, which finally give way to beech and maple (Cowles' unpublished observation). Thus the organisms of such a habitat are subject to increasingly greater degrees

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[1] Address before the American Society of Zoölogists, December, 1907.

of moisture, denser shade, and different materials for abode, including the general absence of mineral soil; in fact all of the factors that are supposed to influence the course and origin of structural characters. The changes brought about by succession, as when the beech forest displaces the oak, are disadvantageous to such tiger beetles as *Cicindela sexguttata* because of the practical disappearance of mineral soil, and the movement of food species from the ground to the vegetation. Experimental conditions could easily be devised which would duplicate and intensify the changes alluded to, while acting upon some favorable organism. If new forms appeared under the experimental conditions any of them *selected a higher level on the plants of the experimental conditions, and possessed any structural characters which enabled them to succeed there*, we would have a case of *true adaptation paralleling the commonest type in nature*. It should be noted also that the fact that elementary adaptations are so often adaptations to stratum speaks in favor of that view of the origin of adaptations advanced by Eigenmann ('08) (selection of suitable habitat by animals possessing adaptation characters). The chief objection to this view seems to have been that animals could not in most cases reach a suitable habitat. We have noted that there are markedly graded (vertical differences) *stratification* conditions of light, temperature, circulation of medium and rate of evaporation. Movement of habitat preferences upward or downward is always a possibility readily attainable. Should an adaptation to a particular stratum become established, new lines of horizontal expansion would be thrown open. Such horizontal extension of range would not usually be accompanied by structural adaptations.

We have doubtless proceeded far enough with the statement of general ecological problems, to note that the training of the ecologist must at present be broad. In the near future, he must specialize upon some aspect of the subject, because it is *unusually large and its concepts especially complex.* At present he is called upon to know general zoölogy, especially general physiology and behavior of organisms. He must have a working knowledge of physiography, climatology, and plant ecology and must be able to analyze, or at least to understand both physical and chemical analysis of soil, water, and air, and be able to experimentally control the factors involved in these. To understand technical ecological work, one must be in very close touch with these fields as well as with special ecological matter. The complexity of the problems involved and the lack of training of zoölogists along these lines, is sufficient reason for the attitude of an occasional zoölogist toward the subject before its problems were clearly formulated.

IV. Summary.

1. Ecological or physiological classification of animals is *based* upon similarities and differences in *physiological life histories, reactions to physical factors* and the general physiology of environic relations, pp. 339, 354.

2. There is an agreement between *mores* of a community due to (*a*) *selection* of habitat through innate characters and (*b*) *modification* of behavior, p. 336.

3. The commonly recognized specificities of behavior are of little significance in ecological classification, p. 338.

4. Adaptation is of questionable significance in ecology; the most common adaptations are to strata or mode of food getting, p. 340.

5. Animal communities of greater magnitude are made up of those of lesser magnitude. The physiological agreement in those of greater magnitude is less close than in those of lower, pp. 354–56.

6. Animal communities are physiologically and genetically (succession) related and their genesis is determined by the genesis of the environment which is usually orthogenetic and converging, p. 359.

7. The relations of ecology to the phenomena of genetics and of adaptation, are not clear; no relations are apparent but actual relations are experimentally determinable.

Hull Zoölogical Laboratories.
University of Chicago,
August 25, 1912.

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